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IMMATURE STAGES OF *LEUCOPIS NINAE* TANASIJTSHUK AND TWO VARIANT POPULATIONS OF *LEUCOPIS GAIMARII* TANASIJTSHUK (DIPTERA: CHAMAEMYIIDAE) FEEDING ON RUSSIAN WHEAT APHID, *DIURAPHIS NOXIA* (MORDVILKO) (HOMOPTERA: APHIDIDAE)

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Abstract.—The present difficulty in identifying adult specimens of *Leucopis* points to a need for additional methods. Characters of the immature stages may be important in this regard, at least for separating certain species and species complexes, although this study indicates possible populational plasticity in one species. Immatures may also be important for systematic studies at higher taxonomic levels. Three populations within *Leucopis* (*s. str.*), including *L. ninae* Tanasijtshuk and two distinct populations of *L. gaimarii* Tanasijtshuk, were found to have reliable characteristics to distinguish them in all immature stages. The characters include the pattern of longitudinal ridges and the structure of pores in the chorionic latticework of eggs, the cephalopharyngeal skeleton morphology and the patterns of surface sculpturing of larvae (any instar) and puparia. The most important characters for larvae and puparia involve the size, density, definition, and contiguity of chaetoids (fleshy, seta-like projections of the integument) covering the body.

Key Words: Chamaemyiidae, *Leucopis,* morphology of immatures

Flies of the family Chamaemyiidae have been recognized as important predators on sternorrhynchous homopterans. However, they are poorly known morphologically in the immature stages, and the adults have been unevenly studied, with the majority of descriptions coming from the Palearctic Region (Tanasijtshuk 1990). There has been little large-scale taxonomic work on the family, except for the revision of the genus *Neoleucopis* Malloch (McAlpine 1971), the revision of the mainly Nearctic genus *Pseudodinia* Coquillett (Barber 1985), and the numerous papers of Tanasijtshuk (especially 1986) for the Palearctic Region. Identifying adults to species is difficult due to their small size (1.0–4.0 mm) and similar external morphology. Features of the male genitalia have been used extensively (Barber 1985, Bennett 1961, McAlpine 1960, 1967, 1971, 1978, McAlpine and Tanasijtshuk 1972, Smith 1963, Tanasijtshuk 1961, 1962, 1965, 1966, 1968a, b, 1970, 1972, 1986, 1996a, b, Tawfik 1966), but there may also be useful characters in the immature stages, and there is an obvious need for associating adults with their respective immatures. This study serves to associate the immature stages and adults of two species, *L. ninae* Tanasijtshuk and *L. gaimarii* Tanasijtshuk, discussed in Gaimari (1993), Gaimari and Turner (1996), and Tanasijtshuk (1996b).

There are detailed descriptions of immature stages for only a small percentage of the known chamaemyiid species. The following is a synoptic list of the detailed descriptions for the immature stages of the Chamaemyiidae: *Chamaemyia flavipalpis* (Haliday) (Raspi 1983), *C. polystigma* Meigen (Sluss and Foote 1973), a *Leucopis* sp. nr. *albipuncta* Zetterstedt (Tracewski 1983), *L. americana* Malloch (Brown and Clark 1956 [as *Leucopina*]), *L. conciliata* McAlpine and Tanasijtshuk (McAlpine and Tanasijtshuk 1972), *L. interruptovittata* Aczél (Raspi 1983), *L. verticalis* Malloch (Sluss and Foote 1971), *Neoleucopis obscura* (Haliday) (Brown and Clark 1956, Trägårdh 1931), *N. pinicola* Malloch (Clark and Brown 1957, Sluss and Foote 1973 [as *L.* (*N.*) *pinicola*]), *Parochthiphila coronata* (Loew) (Raspi 1983), and *Pseudodinia pruinosa* Melander (Barber 1985). The morphology of eggs has been described for *Chamaemyia flavipalpis* (Haliday) and *Parochthiphila coronata* (Loew) (Mazzini and Raspi 1983), and generally for *Leucopis* Meigen, *Chamaemyia* Panzer, *Parochthiphila* Czerny, and *Acrometopia* Schiner (Tanasijtshuk 1974). Additionally, Bennett (1961), Maple (1934), and Tanasijtshuk (1959) discussed the immature stages for several *Leucopis* species, and Ferrar (1987) provides a synopsis of descriptions, including partial descriptions for the immatures of some species in the family. The following descriptions will add to the morphological information on the immature stages of *Leucopis*. They will also provide a partial framework of characters for systematic studies necessary for distinguishing genera, species groups, and species in the various immature stages.

Materials and Methods

Three populations of *Leucopis* (*s. str.*) were used in this study: *L. ninae* from Skopje, Macedonia (approximately 42°N 21°E), and two populations of *L. gaimarii* from eastern Washington. The 'Central Ferry' population of *L. gaimarii* (*L.* sp. #1 of Gaimari 1993) originated in Washington, Garfield County, Central Ferry, USDA-ARS Research Farm (46°37′N 117°49′W; elevation 195 m), swept in July 1991 from cereal ryegrass, *Secale cereale* Linnaeus (Poaceae), infested with Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Homoptera: Aphididae). The 'Anatone' population of *L. gaimarii* (*L.* sp. #2 of Gaimari 1993) originated in Washington, Asotin County, 0.6 km west Anatone (46°08′N 117°08′W; elevation 1160 m), swept in August 1991 from *D. noxia*-infested wheat, *Triticum aestivum* Linnaeus (Poaceae). Tanasijtshuk (1966, 1986, 1996b) discussed the adult stage of *L. ninae* and provided figures of the male terminalia, and *L. gaimarii* is described for the first time in Tanasijtshuk (1996b).

Specimens of all life stages and instars of the three populations were obtained from living cultures in the Northwest Biological Control Insectary and Quarantine facility at Washington State University. Information on the origins and maintenance of these colonies can be found in Gaimari (1993). The present work describes the morphology in all immature stages and instars of *L. ninae* and both populations of *L. gaimarii*. Morphological data not repeated in the description of *L. gaimarii* (using the 'Central Ferry' population as the standard) are the same as in *L. ninae*. Differences between the two populations of *L. gaimarii* are noted in the text, i.e. variations and figures of the 'Anatone' population are set off in brackets.

Live larvae ($n > 150$) were measured daily to provide a full size range for each instar. Because they extend and retract during movement, we adopted a standardized method for measurement where each larva was measured when fully extended to determine the maximum body length.

For scanning electron microscope study, specimens were prepared in the following manner. All immature stages were killed in 70% ethyl alcohol. Eggs and larvae were dehydrated through an ethanolic step series, increasing the concentration of alcohol by five percent every eight hours until reaching 100%. Specimens remained in 100% ethyl alcohol for at least eight hours before being desiccated under CO_2 in a critical point dryer. This reduced the distortion that normally occurs when soft-bodied specimens are preserved in ethyl alcohol (Postek et al. 1980, Stehr 1987). Puparia were sufficiently sclerotized to be air dried without distortion. Specimens were attached to stubs using double-stick tape and plasma sputter coated with a 30 nm gold layer. Images were photographed through the microscope running at an accelerating voltage of 20 kV. Gaimari (1994) found that live puparia were able to survive the harsh conditions within the plasma sputter coater and the scanning electron microscope.

Larval cephalopharyngeal skeletons were acquired from larval exuviae, eclosed puparia, and living specimens. Larval exuviae and puparia were placed in glycerin on a drop-center slide and viewed under phase-contrast microscopy. Living larvae were killed and preserved in 70% ethyl alcohol. The integument was cleared by cutting the larva in half and soaking the anterior end in cold 10% sodium hydroxide overnight. The specimens were then rinsed for 10 minutes with water and acidified in a 0.5–1.0% acetic acid solution for one hour. Any remaining tissue around the skeleton was teased out under a dissecting microscope. The cephalopharyngeal skeletons were transferred into glycerin on a drop-center slide and viewed as above, and drawn with the help of a camera lucida.

Morphology and Terminology

Basic terminology for morphology is according to Teskey (1981). The following are some definitions and clarifications of terminology used in the present work.

In reference to larval and puparial segmentation, we refer to the thoracic segments as 1–3, and the abdominal segments as I–VIII, anterior to posterior. Ranges and means are given in the form "range, mean," e.g. 0.11–0.16, 0.14 mm.

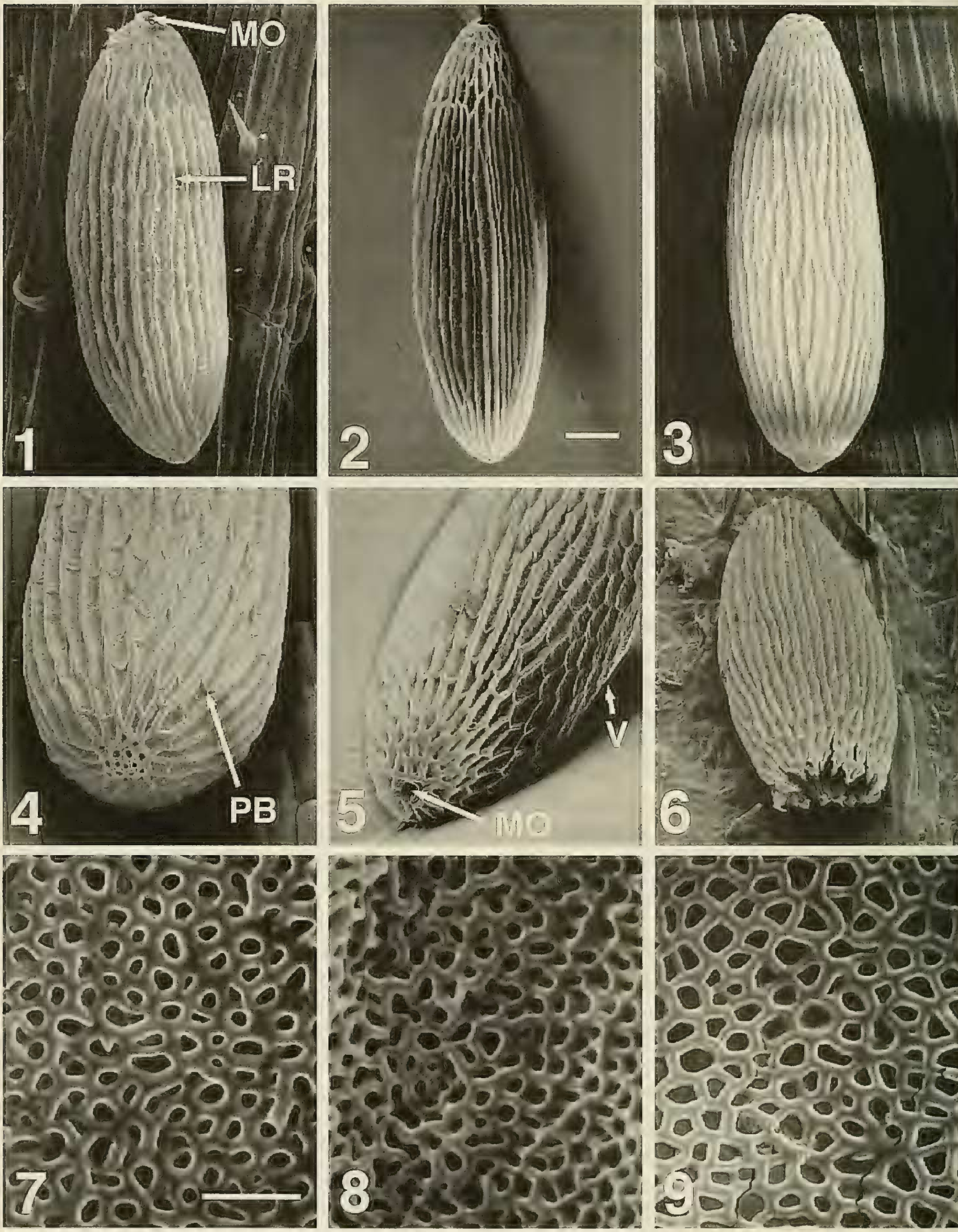
The posterior end of the egg has numerous openings (Fig. 4) of as yet unknown function. Some authors (Barber 1985, Mazzini and Raspi 1983, Tanasijtshuk 1974, Tracewski 1983) have suggested that these openings represent micropyles. However, Ferrar (1987) points out that in the cyclorrhaphous Diptera, the micropyles are always at the anterior pole of the egg, which is the eclosion end. This is consistent with earlier interpretations by Sluss and Foote (1971, 1973) in their treatments of the Chamaemyiidae.

Chaetoids are fleshy, seta-like projections of the larval integument (e.g. Figs. 18–26). They vary among species, and among instars, as to their contiguity, density, size, and definition. Measurement of "chaetoid density" on the anterior and posterior pseudosegments of segment III was accomplished by using the enlarged chaetoid row of the middle pseudosegment (as in Fig. 19) as a frame of reference; the middle four set off the area counted.

Results

Egg

Leucopis ninae.—Length 0.47–0.57, 0.52 mm (n > 50); maximum width 0.17–0.22, 0.20 mm; live color off-white to white; subcylindrical; posterior end bluntly rounded; anterior end slightly tapered (Fig. 1); posterior end with 5–14 openings (as in Fig. 4), each encircled by a ring of small pores; anterior end with single, rounded micropylar opening (as in Fig. 5); chorion highly sculptured (Fig. 1), dorsum convex, with longitudinal ridges distinct and subparallel; 13–15 ridges visible at widest portion of dorsal aspect; perpendicular connective bridges join major ridges (as in Fig. 4); ridges within transverse median area commonly anastamosing, posterior end with frequent anastamosing, anterior end with hexagonal arrangement; venter slightly flattened, with similar hexagonal arrangement, except medially, where it becomes less pronounced (as in Fig. 5); eclosed egg with opening irregular and jagged (as in Fig. 6) due to first instar tearing chorion with mouth hooks to escape; pores of chorionic lattice-



Figs. 1–9. Egg stage. 1, *Leucopis ninae,* dorsal. 2, *L. gaimarii* 'Central Ferry,' dorsal (scale bar = 0.05 mm). 3, *L. gaimarii* 'Anatone,' dorsal. 4, *L. gaimarii* 'Anatone,' anterior. 5, *L. gaimarii* 'Central Ferry,' posterior. 6, *L. gaimarii* 'Anatone,' anterior, post-eclosion. 7, *L. ninae,* chorionic latticework (scale bar = 2.0 μm). 8, *L. gaimarii* 'Central Ferry,' chorionic latticework. 9, *L. gaimarii* 'Anatone,' chorionic latticework. Abbreviations: LR = longitudinal ridge; MO = micropylar opening; PB = perpendicular connective bridge; V = venter.

work (Fig. 7) possibly represent aeropyles (Tanasijtshuk 1974), usually not as wide as inter-pore distance, smooth and rounded; pore diameter 0.20–0.60, 0.42 μm (n > 50 pores); over 20 pores per 10 μm^2 area.

Leucopis gaimarii.—Length 0.45–0.55, 0.52 [0.42–0.52, 0.47] mm (n > 50); maximum width 0.15–0.22 [0.16–0.20], 0.19 mm; chorion (Fig. 2 [3]) with 14–17 [13–15] longitudinal, dorsal ridges visible at widest portion of dorsal aspect; ridges within transverse median area closely parallel and unbranched [subparallel and commonly anastamosing]; pores of chorionic latticework (Fig. 8 [9]) smaller and rounded [with angular appearance], usually slightly wider than inter-pore distance; pore diameter 0.10–0.40, 0.26 [0.30–0.90, 0.51] μm (n > 50 pores); over 30 [20] pores per 10 μm^2 area.

First Larval Instar

Leucopis ninae.—Length 0.50–1.25 mm (n > 100); maximum width 0.20–0.35 mm; whitish to slightly translucent with sparse, milky-white globules under integument; darkened gut material visible through integument in fed individuals; body segments (in all larval instars and puparium) variously studded with chaetoids.

Dorsally (Fig. 10), larva fusiform, tapered more anteriorly than posteriorly; narrowed posteriorly from segments V–VIII and anteriorly from segments IV–1; largest segments (IV and V) subequal in size; segmentation clearly visible; segments 2–VII divided into 3 pseudosegments by secondary annulations (Fig. 18); middle pseudosegment (Fig. 18) with transverse row of 6 distinctly enlarged chaetoids (labeled in Fig. 19); additional enlarged chaetoid isolated beyond lateral end of row (Fig. 18); middle pseudosegment not extended laterally beyond dorsal aspect, but appears enclosed by anterior and posterior pseudosegments; anterior and posterior pseudosegments with numerous, small, poorly-defined, separated chaetoids; chaetoid density (as defined in Morphology and Terminology) 18–22, 19 chaetoids (n > 10).

Laterally (as in Fig. 13), tapering consistent with dorsal aspect; pseudosegmentation not apparent; segments 2–VII with small chaetoids extending slightly beyond large chaetoid row of middle pseudosegment of dorsal aspect (Fig. 29); distinct swelling with central pit visible beyond large chaetoid row; tubercles dorsad and ventrad to swelling indistinct; low, creeping welt-like mounds arise ventral to swelling on segments 3–VII.

Cephalic segment fully retractable (as in Fig. 49); antennal papillae distinct and elongated; maxillary sensory papillae evident beneath as pair of large disks, separated by vertical, median groove; pair of small papillae arise below these and lateral to preoral cavity; cephalopharyngeal skeleton as in Fig. 38; gular region with incomplete U-shaped collar or cephalic ring (Bennett 1961, Gaimari 1993, Hennig 1952, Maple 1934, Smith 1989).

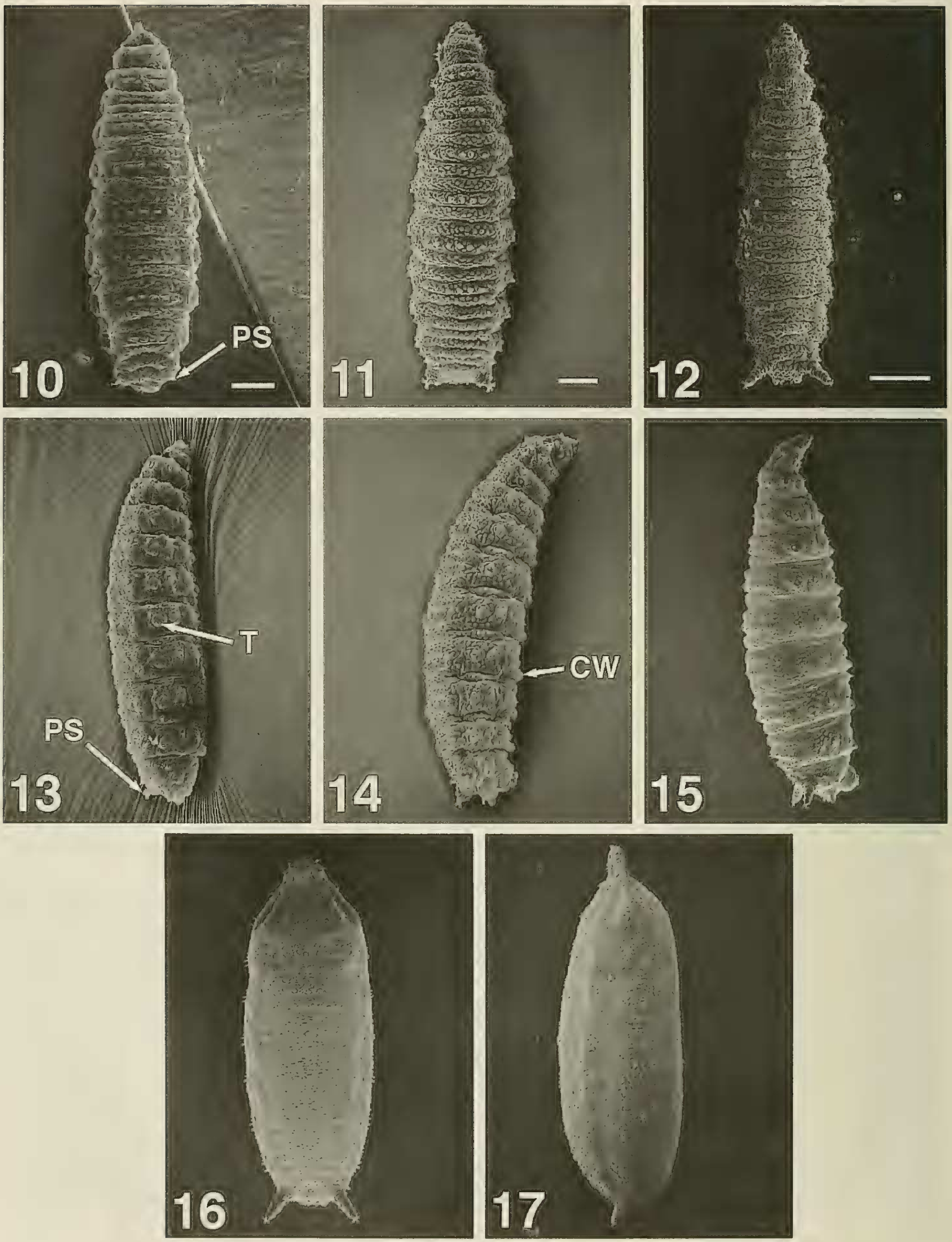
Anterior spiracles absent; posterior spiracles on short, tubular stalks, slightly diverging at posterolateral corners of tergite VIII (Fig. 62); each bilobed with transverse, distal slit on each lobe (as in Fig. 53).

Segment VIII divided dorsally into 2 pseudosegments, each with few, poorly-defined, small chaetoids (Fig. 62); posterior pseudosegment with about 20 chaetoids between posterior spiracular processes; caudal area with 2 small, indistinct chaetoids above and between paired, projecting tubercles; anus situated below.

Leucopis gaimarii.—Length 0.55–1.25 [0.50–1.25] mm (n > 100); maximum width 0.15–0.35 [0.15–0.30] mm.

Dorsally, anterior and posterior pseudosegments with numerous, small, poorly-defined [well-defined], contiguous (pattern appearing braided) chaetoids (Fig. 19 [20]); chaetoid density 20–24, 22 [13–17, 15] chaetoids (n > 10).

Laterally [Fig. 13], swelling with enlarged tubercles: 1 dorsad (consisting of 2 enlarged, fused chaetoids) and 1 ventrad to pit (Fig. 30 [31]).



Figs. 10–17. Larval and puparial habitus. 10, *Leucopis ninae,* dorsal first instar (scale bar = 0.1 mm). 11, *L. gaimarii* 'Central Ferry,' dorsal second instar (scale bar = 0.1 mm). 12, *L. gaimarii* 'Anatone,' dorsal third instar (scale bar = 0.5 mm). 13, *L. gaimarii* 'Anatone,' lateral first instar. 14, *L. gaimarii* 'Central Ferry,' lateral second instar. 15, *L. ninae,* lateral third instar. 16, *L. ninae,* dorsal puparium. 17, *L. gaimarii* 'Central Ferry,' lateral puparium. Abbreviations: CW = creeping welt; PS = posterior spiracle; T = tubercle.

Cephalopharyngeal skeleton as in Fig. 39 [40].

Segment VIII with posterior pseudosegment having about 25 [20] small, well-defined chaetoids between posterior spiracular processes (Fig. 63).

Second Larval Instar

Leucopis ninae.—Length 1.30–2.50 mm (n > 100); maximum width 0.30–0.70 mm; whitish to slightly translucent with scattered, milky-white globules beneath integument; blackened gut visible through integument.

Dorsally (as in Fig. 11), larva similar to first instar, except narrowed posteriorly from segments VI–VIII and anteriorly from segments IV–1; largest segments (IV–VI) subequal in size; middle pseudosegment (Fig. 21) with scattered, small, poorly-defined chaetoids and transverse row of 6 elongated, spinule-like chaetoids protruding from low, disk-like elevations; additional spinule-like chaetoid isolated beyond lateral end of row; middle pseudosegment not extended laterally beyond dorsal aspect, but appears enclosed by anterior and posterior pseudosegments; anterior and posterior pseudosegments with scattered, small, poorly-defined, separated chaetoids; chaetoid density 16–21, 18 chaetoids (n > 10).

Laterally (as in Fig. 14), tapering consistent with dorsal aspect; pseudosegmentation not apparent; segments 2 and 3 each with 3 elongated, spinule-like chaetoids in triangular arrangement (as in Fig. 56); segments I–VII each with lateral swelling bearing central pit and sparse, small, poorly-defined chaetoids (Fig. 32); swelling with 2 spinule-like chaetoids dorsad and 1 ventrad to pit, also visible in dorsal aspect.

Ventrally (Fig. 32), 3 pseudosegments evident on segments 2–VII; posterior pseudosegment with large, paired, creeping welt-like mounds; anterior pseudosegment with smaller, second pair of mounds placed medially to larger mounds; middle pseudosegment with elongated, spinule-like, ventrolateral chaetoid beneath ventrolateral pit.

Cephalic segment (Fig. 50) as in 1st instar, except maxillary sensory papillae evident as a pair of small, raised disks, separated by vertical, median groove; pair of larger papillae below these and laterad to preoral cavity; cephalopharyngeal skeleton as in Fig. 41; gular region with incomplete, U-shaped collar or cephalic ring (Fig. 42).

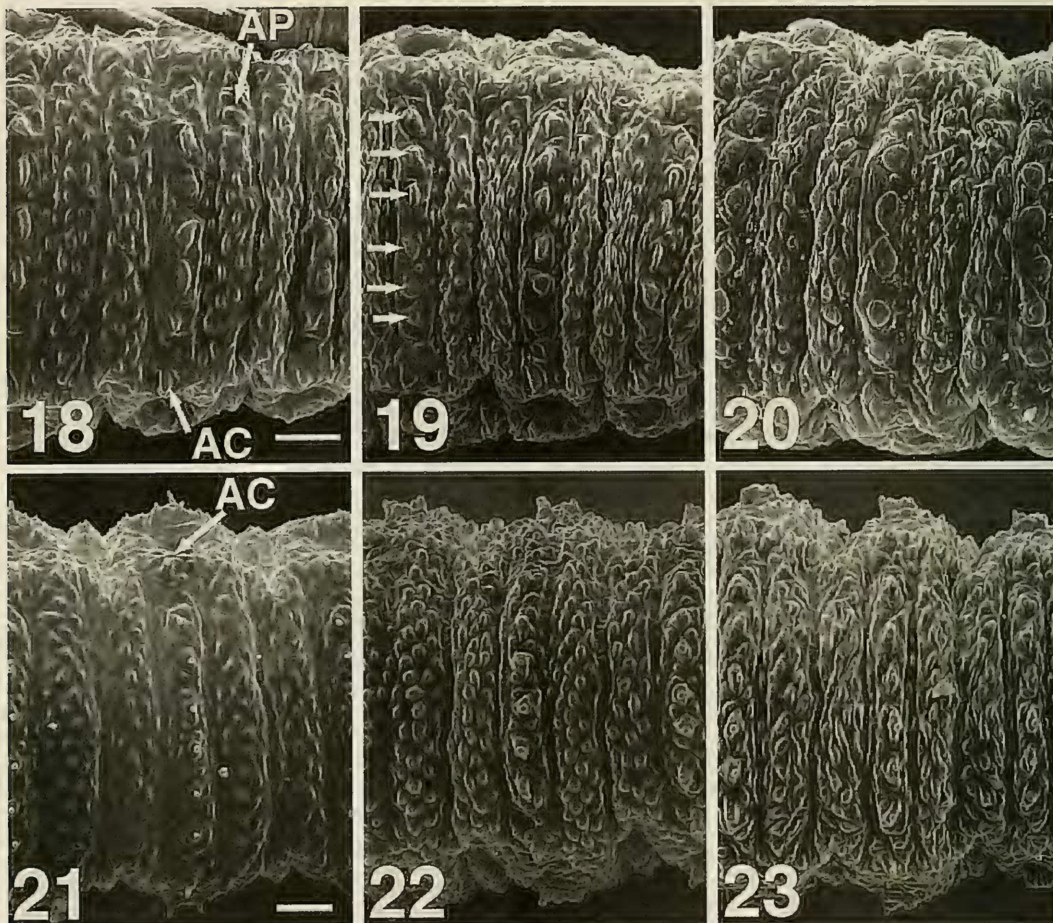
Anterior spiracles directed forward from posterolateral portion of segment 1 (as in Fig. 56); each 3 or 4 lobed, or mixed, spread fan-like with single, transverse, distal slit in each lobe; single, circular opening (probably the ecdysial scar) basal to lobes and posterior on spiracular base; posterior spiracle trilobed, mounted on a raised, quadrangular prominence with short, wide base (Fig. 54); base covered with small chaetoids, similar to those of dorsal aspect; lobes each bearing single, transverse, distal slit; single, circular opening (probably the ecdysial scar) basal to lobes.

Segment VIII deeply divided dorsally into 2 pseudosegments, each with small, scattered chaetoids (Fig. 64); posterior pseudosegment with about 14 small, poorly-defined chaetoids between posterior spiracular processes; laterally, 3 elongated, spinule-like chaetoids present in triangular arrangement; caudal area with few chaetoids, except for 2 small chaetoids above and between paired, projecting tubercles. Anus situated below.

Leucopis gaimarii.—Length 1.15–2.55 [1.05–2.45] mm (n > 100); maximum width 0.25–0.65 [0.20–0.60] mm.

Dorsally (Fig. 11), middle pseudosegment with scattered, small, well-defined [poorly-defined] chaetoids and transverse row of 6 enlarged, well-defined [poorly-defined], stubby chaetoids; additional enlarged, stubby chaetoid beyond lateral end of row; anterior and posterior pseudosegments with numerous, small, crowded (but separated) [contiguous (pattern appearing braided)], well-defined [poorly-defined] chaetoids (Fig. 22 [23]); chaetoid density 20–25, 23 [18–21, 20] chaetoids (n > 10).

Laterally [Fig. 14], segments 2 and 3 each with 3 enlarged, stubby chaetoids in



Figs. 18–23. Segment III, dorsal (anterior to right). 18, *Leucopis ninae,* first instar (scale bar = 0.05 mm). 19, *L. gaimarii* 'Central Ferry,' first instar. 20, *L. gaimarii* 'Anatone,' first instar. 21, *L. ninae,* second instar (scale bar = 0.05 mm). 22, *L. gaimarii* 'Central Ferry,' second instar. 23, *L. gaimarii* 'Anatone,' second instar. Abbreviations: AC = additional enlarged chaetoid beyond lateral end of row; AP = anterior pseudosegment; unlabelled arrows = enlarged chaetoid row of middle pseudosegment of segment IV.

triangular arrangement (Fig. 56); lateral swelling with 2 enlarged, stubby chaetoids on raised area dorsad and 1 ventrad to pit, also visible in dorsal aspect; swelling with dense [sparse], small, well-defined [poorly-defined] chaetoids (Fig. 33 [34]).

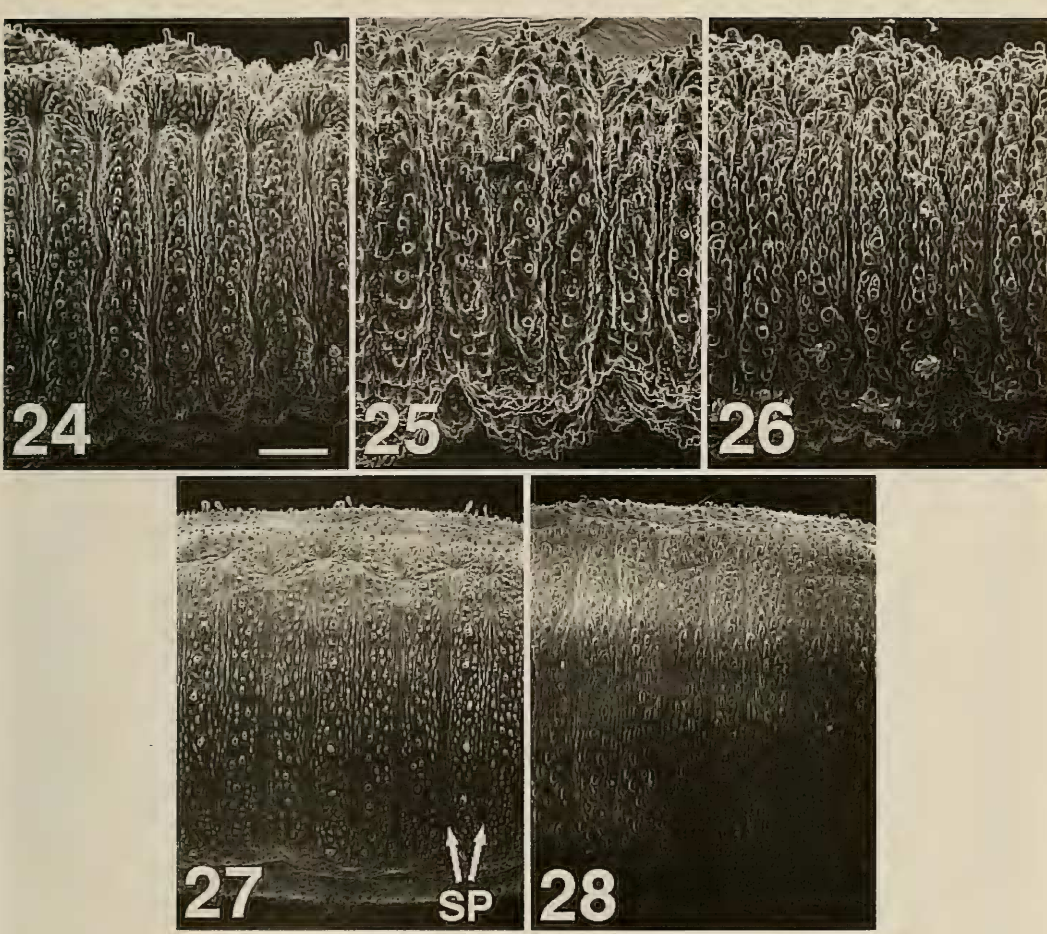
Ventrally, pseudosegmentation faint; middle pseudosegment with enlarged, stubby, ventrolateral chaetoid beneath ventrolateral pit (Fig. 33 [34]).

Cephalopharyngeal skeleton as in Fig. 43 [44]; gular region as in *L. ninae.*

Segment VIII with posterior pseudosegment having about 25 [20] small, well-defined, crowded [contiguous] chaetoids between posterior spiracular processes (Fig. 65); laterally, 3 enlarged, stubby chaetoids present in triangular arrangement.

Third Larval Instar

Leucopis ninae.—Length 2.35–4.25 mm (n > 100); maximum width 0.55–1.20 mm; slightly translucent with many milky-white globules under integument, giving body white appearance; black gut contents visible through integument, especially posteriorly.



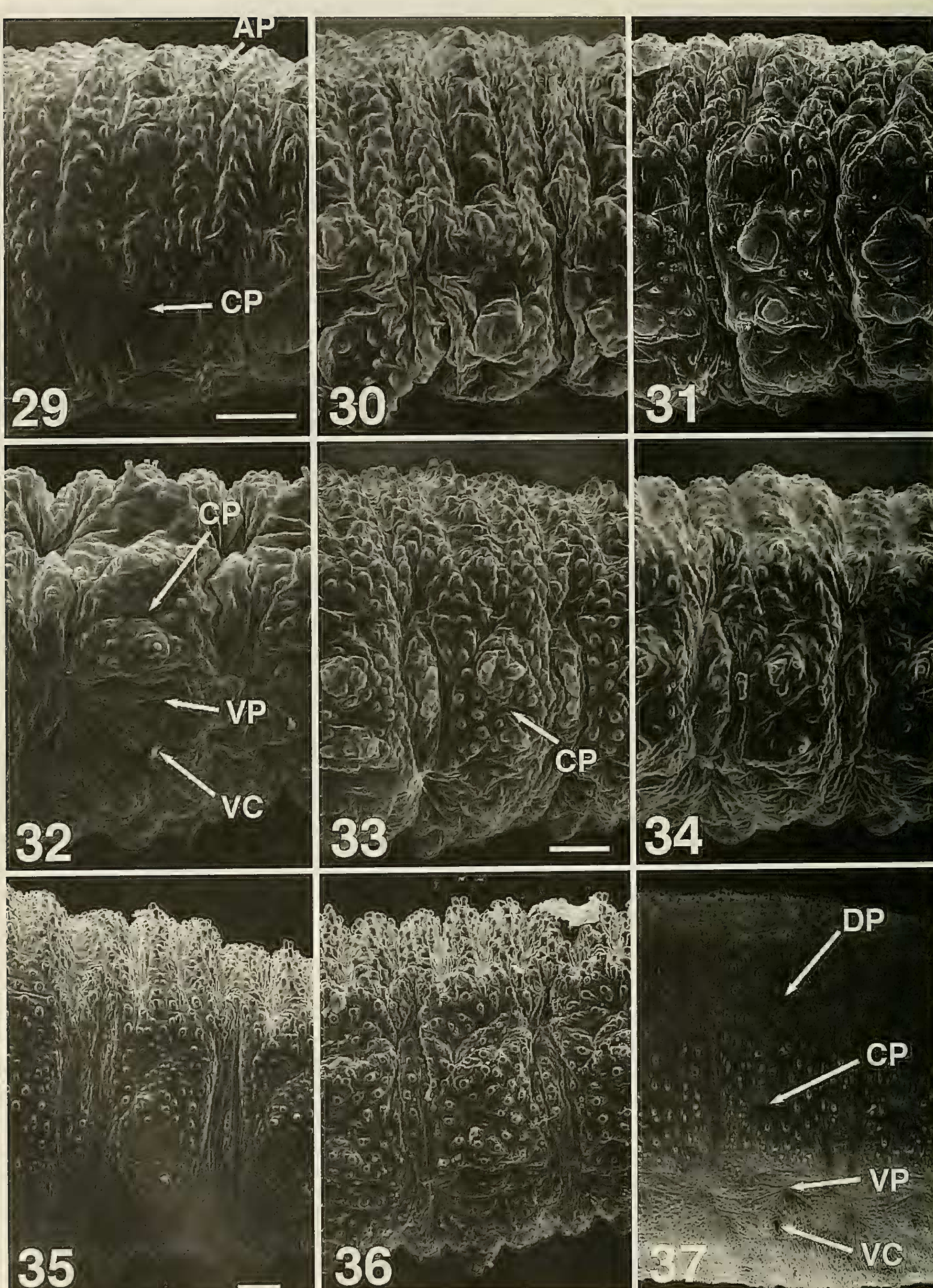
Figs. 24–28. Segment III, dorsal (anterior to right). 24, *Leucopis ninae,* third instar (scale bar = 0.1 mm). 25, *L. gaimarii* 'Central Ferry,' third instar. 26, *L. gaimarii* 'Anatone,' third instar. 27, *L. ninae,* puparium. 28, *L. gaimarii* 'Anatone,' puparium. Abbreviation: SP = shallow pits at lateral end of enlarged chaetoid row.

Dorsally (as in Fig. 12), similar to second instar, except middle pseudosegment (Fig. 24) with numerous, small, well-defined chaetoids and transverse row of 6 distinctly elongated, spinule-like chaetoids; single, additional spinule-like chaetoid isolated beyond lateral ends of row; segments 2 and 3 with longer chaetoids in row (see Fig. 57); middle pseudosegment not extended laterally beyond dorsal aspect, but appearing enclosed by deep groove; anterior and posterior pseudosegments with numerous, small, well-defined, separated chaetoids; chaetoid density 42–48, 46 chaetoids ($n > 10$).

Laterally (Figs. 15 and 57), similar to second instar, except lateral swelling with numerous, small, distinct, separated chaetoids (Fig. 35).

Ventrally, similar to second instar, except surface densely covered with tiny, well-defined chaetoids (Fig. 35); ventrolateral chaetoids forming distinct longitudinal row (Fig. 66).

Cephalic segment (Fig. 51) as in 2nd instar, except antennal papillae 2-segmented, basal segment disk-like, distal segment elongated; maxillary sensory papillae evident as pair of small disks separated by wide, vertical, median furrow; pair of larger papillae below these and lateral to preoral



Figs. 29–37. Segment III, lateral (anterior to right). 29, *Leucopis ninae,* first instar (scale bar = 0.05 mm). 30, *L. gaimarii* 'Central Ferry,' first instar. 31, *L. gaimarii* 'Anatone,' first instar. 32, *L. ninae,* second instar (note, specimen more rotated than in other figures). 33, *L. gaimarii* 'Central Ferry,' second instar (scale bar = 0.05 mm). 34, *L. gaimarii* 'Anatone,' second instar. 35, *L. ninae,* third instar (scale bar = 0.1 mm). 36, *L.*

cavity; cephalopharyngeal skeleton as in Fig. 45; gular region with incomplete, U-shaped collar or cephalic ring (as in Fig. 46).

Anterior spiracles as in second instar, only larger (Fig. 57); posterior spiracles trilobed, situated distally on long, tubular base (Fig. 55) which may be partially darkened and sclerotized near tip; bases separated by 0.20–0.45 mm (n > 10); covered with small chaetoids, similar to those of dorsal aspect; lobes as in second instar.

Segment VIII shallowly divided dorsally into 2 pseudosegments, each with small, scattered chaetoids (Fig. 66); posterior pseudosegment with about 30 well-defined, separated chaetoids between and continuing partially up on posterior spiracular processes; laterally, as in second instar, except caudal area with 2 elongated, spinule-like chaetoids above and between paired, projecting tubercles.

Leucopis gaimarii.—Length 2.10–4.20 [2.40–4.30] mm (n > 100); maximum width 0.55–1.20 mm.

Dorsally [Fig. 12], middle pseudosegment with scattered, poorly-defined [and contiguous] chaetoids subequal in size to transverse row of 6 enlarged, stubby chaetoids; additional indistinctly enlarged, stubby chaetoid isolated beyond lateral end of row; anterior and posterior pseudosegments with [numerous] poorly-defined, separated [contiguous (pattern appearing braided)] chaetoids, subequal in size to chaetoids of middle pseudosegment (Fig. 25 [26]); chaetoid density 16–23, 19 [22–26, 23] chaetoids (n > 10).

Laterally, segments 2 and 3 each with 3 enlarged, stubby chaetoids in triangular arrangement; segments I–VII each with lateral swelling bearing central pit and numerous, well-defined, separated chaetoids [Fig. 36]; swelling with 2 enlarged, stubby chaetoids dorsad and 1 ventrad to pit, also visible in dorsal aspect.

Ventrally, surface sparsely covered with tiny, scattered, poorly-defined chaetoids [Fig. 36]; middle pseudosegment with enlarged, stubby, ventrolateral chaetoid beneath ventrolateral pit, forming indistinct, longitudinal row.

Cephalopharyngeal skeleton as in Fig. 47 [46, 48].

Segment VIII, laterally with 3 enlarged, stubby chaetoids present in triangular arrangement; caudal area with few chaetoids, except for 2 enlarged, stubby chaetoids above and between paired, projecting tubercles.

Puparium

Leucopis ninae.—Length 2.45–2.90, 2.65 mm (n > 50); maximum width 0.87–1.15, 1.04 mm; upon pupariation integument off-white and slightly translucent, but within a short time hardens and darkens to reddish-brown, although puparial integument partially transparent so that parts of developing pupa are visible.

Dorsally (Fig. 16), subovate; posterior end bluntly rounded; anterior end abruptly tapered from segment I forward; segments distinct, but not deeply divided; segments 2–VII each divided into 3 pseudosegments with shallow, transverse depressions (Fig. 27); middle pseudosegment as in third instar; lateral end of transverse row of 6 distinctly elongated, spinule-like chaetoids with 2 shallow pits (Figs. 17 and 27); segments 2–I with elongated, spinule-like chaetoids in transverse row; anterior and posterior pseudosegments as in third instar; chaetoid density 42–48, 45 chaetoids (n > 10).

Laterally (as in Fig. 17), highly convex above and distinctly flattened below; anteriorly, segments I–1 become conspicuously

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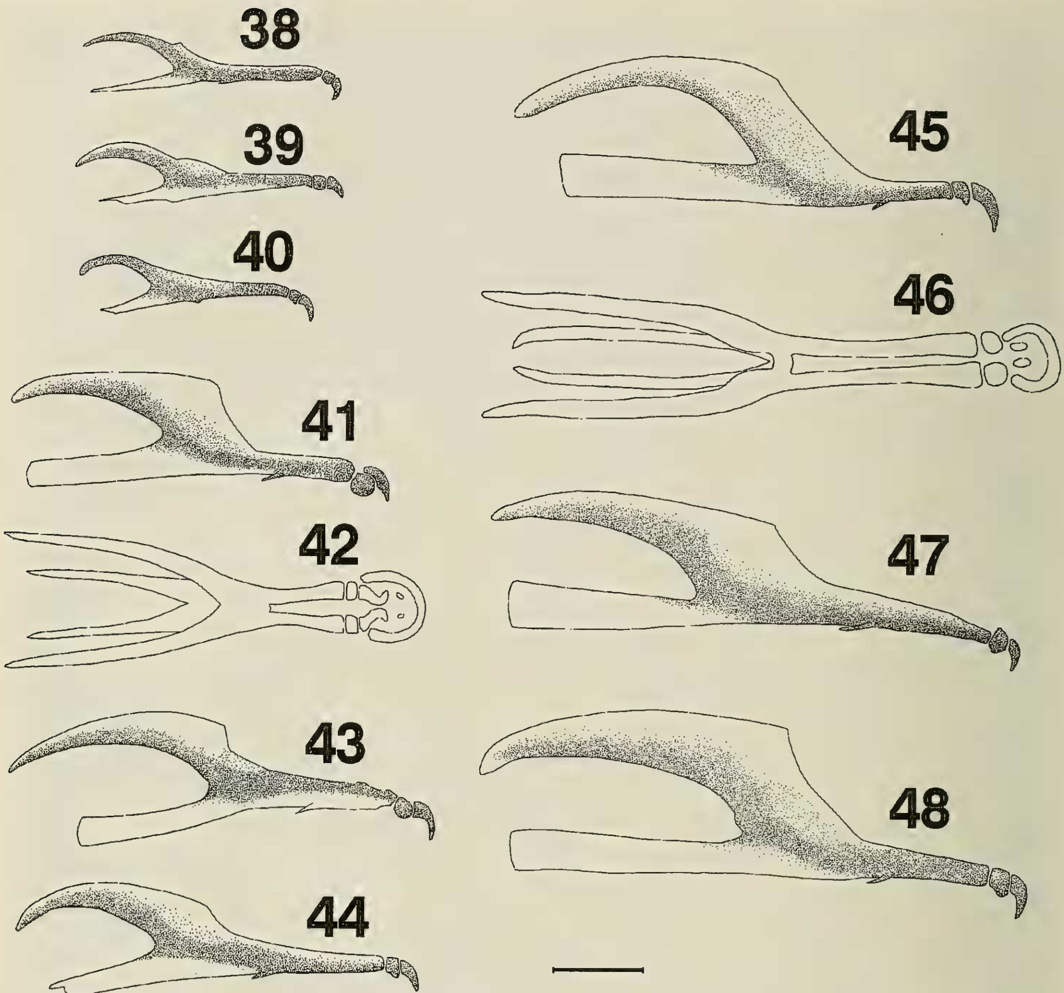
gaimarii 'Anatone,' third instar. 37, *L. ninae,* puparium. Abbreviations: AP = anterior pseudosegment; CP = central pit of swelling; DP = dorsolateral pit; VC = ventrolateral chaetoid; VP = ventrolateral pit.

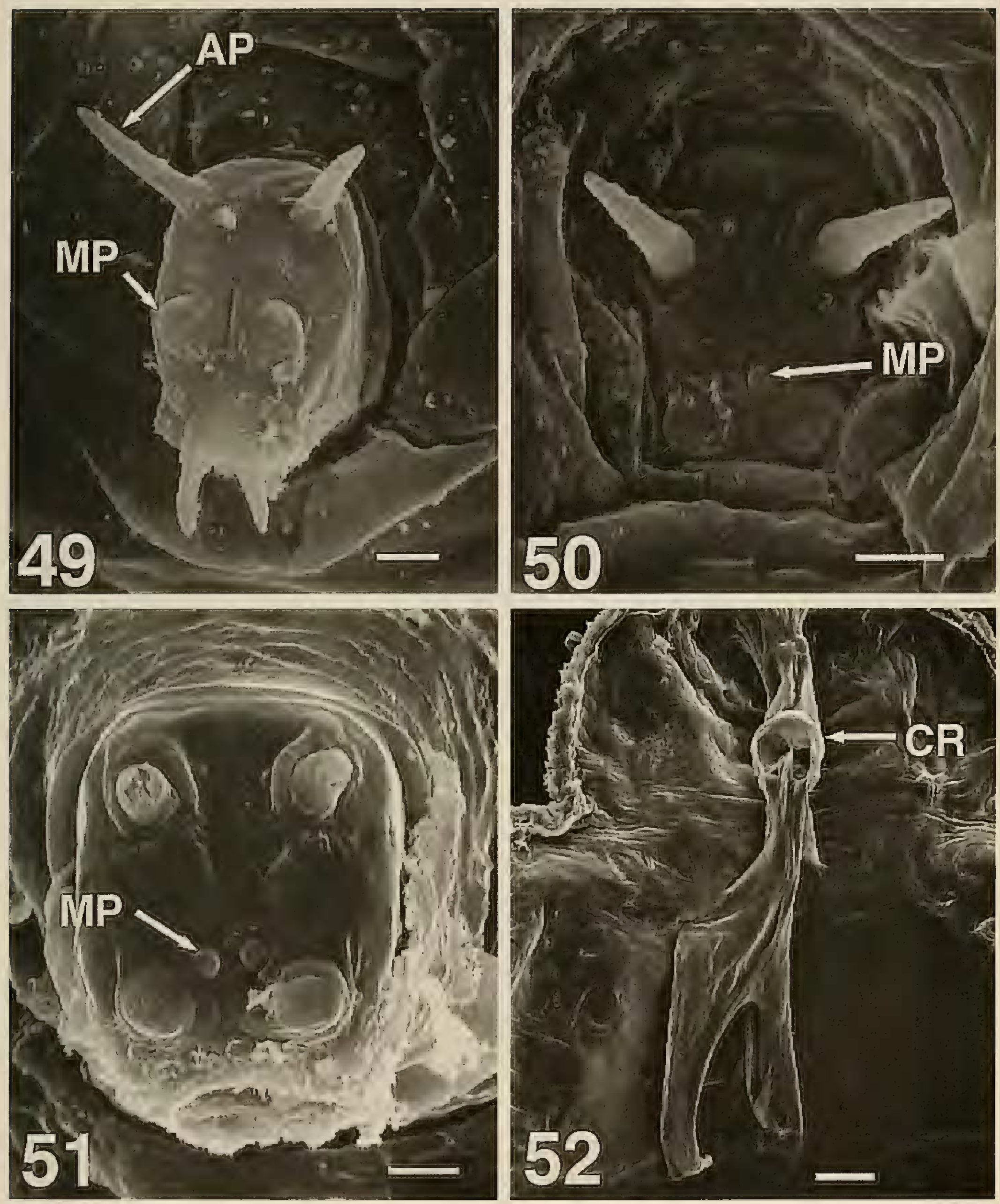


Figs. 38–48. Cephalopharyngeal skeleton. 38, *Leucopis ninae,* first instar. 39, *L. gaimarii* 'Central Ferry,' first instar. 40, *L. gaimarii* 'Anatone,' first instar. 41, *L. ninae,* second instar. 42, *L. ninae,* dorsal second instar. 43, *L. gaimarii* 'Central Ferry,' second instar. 44, *L. gaimarii* 'Anatone,' second instar. 45, *L. ninae,* third instar. 46, *L. gaimarii* 'Anatone,' dorsal third instar. 47, *L. gaimarii* 'Central Ferry,' third instar. 48, *L. gaimarii* 'Anatone,' third instar. Scale bar = 0.05 mm.

flattened dorsoventrally; pseudosegmentation not apparent; segments I–VII each with indistinct, lateral swelling (Fig. 37); swelling sparsely covered with small, well-defined chaetoids, and 3 elongated, spinule-like chaetoids in triangular arrangement around central pit: 2 above and 1 below; elongated chaetoids prominent in dorsal aspect; dorsolateral pit above central pit of swelling and lateral to paired depressions at end of transverse row of chaetoids on middle pseudosegment of dorsal aspect.

Ventrally (Fig. 37), 3 pseudosegments apparent, divided by shallow, transverse depressions; creeping welts absent due to inflation of integument; pseudosegments densely covered with tiny, separated chaetoids; middle pseudosegment with elongated, spinule-like, ventrolateral chaetoid beneath ventrolateral pit.

Head region appearing wrinkled (Fig. 59); cephalic segment retracted into segment 1 and not visible; segments 2 and 3 surrounded by elongated, spinule-like chae-



Figs. 49–52. Cephalic structures. 49, *Leucopis gaimarii* 'Anatone,' first instar, cephalic segment (scale bar = 0.005 mm). 50, *L. ninae,* second instar, cephalic segment (scale bar = 0.01 mm). 51, *L. ninae,* third instar, cephalic segment (scale bar = 0.01 mm) (note: AP appears broken off). 52, *L. ninae,* cephalopharyngeal skeleton from emerged puparium (scale bar = 0.05 mm). Abbreviations: AP = antennal papilla; CR = cephalic ring; MP = maxillary sensory papilla.

toids; cephalopharyngeal skeleton of third instar visible on inside ventral portion of anterior segments after adult emergence; incomplete collar, or cephalic ring, visible (Fig. 52).

Anterior spiracles either 3-lobed (as in Figs. 58 and 59), 4-lobed (as in Fig. 61), or mixed (as in Fig. 60), as in second and third instar, except protracted farther and more conspicuous; posterior spiracles (Fig. 67) as in third instar, but fully sclerotized; bases separated by 0.18–0.35, 0.27 mm (n > 50).

Segment VIII shallowly divided dorsally into 2 pseudosegments, each with small, scattered chaetoids (Fig. 67); posterior pseudosegment with about 30 small, well-defined, separated chaetoids between and continuing partially up on posterior spiracular processes; laterally, 3 elongated, spinule-like chaetoids present in triangular arrangement; caudal area with few chaetoids, except 2 slightly enlarged chaetoids between and above paired, projecting tubercles; anus situated below; hardened droplet of black, shiny exudate from anus usually present (not shown in Figures), resulting from gut contents purged prior to pupariation.

Leucopis gaimarii.—Length 2.30–2.75, 2.56 [2.35–2.90, 2.62] mm (n > 50); maximum width 0.80–1.20, 1.03 [0.90–1.20, 1.05] mm.

Dorsally, middle pseudosegment with numerous, poorly-defined, contiguous and flattened chaetoids subequal in size to transverse row of 6 indistinctly enlarged chaetoids [Fig. 28]; additional enlarged chaetoid isolated beyond lateral end of row; anterior and posterior pseudosegments with poorly-defined, contiguous and flattened chaetoids; chaetoid density 16–23, 21 [22–26, 24] chaetoids (n > 10).

Laterally (Fig. 17), lateral swelling densely [sparsely] covered with small, well-defined chaetoids, and 3 slightly enlarged, blunt chaetoids in triangular arrangement around central pit: 2 above and 1 below; enlarged chaetoids visible in dorsal aspect, but short and stubby.

Ventrally, middle pseudosegment with indistinctly enlarged, blunt, ventrolateral chaetoid beneath ventrolateral pit.

Posterior spiracles with bases separated by 0.28–0.38, 0.31 [0.29–0.44, 0.35] mm (n > 50).

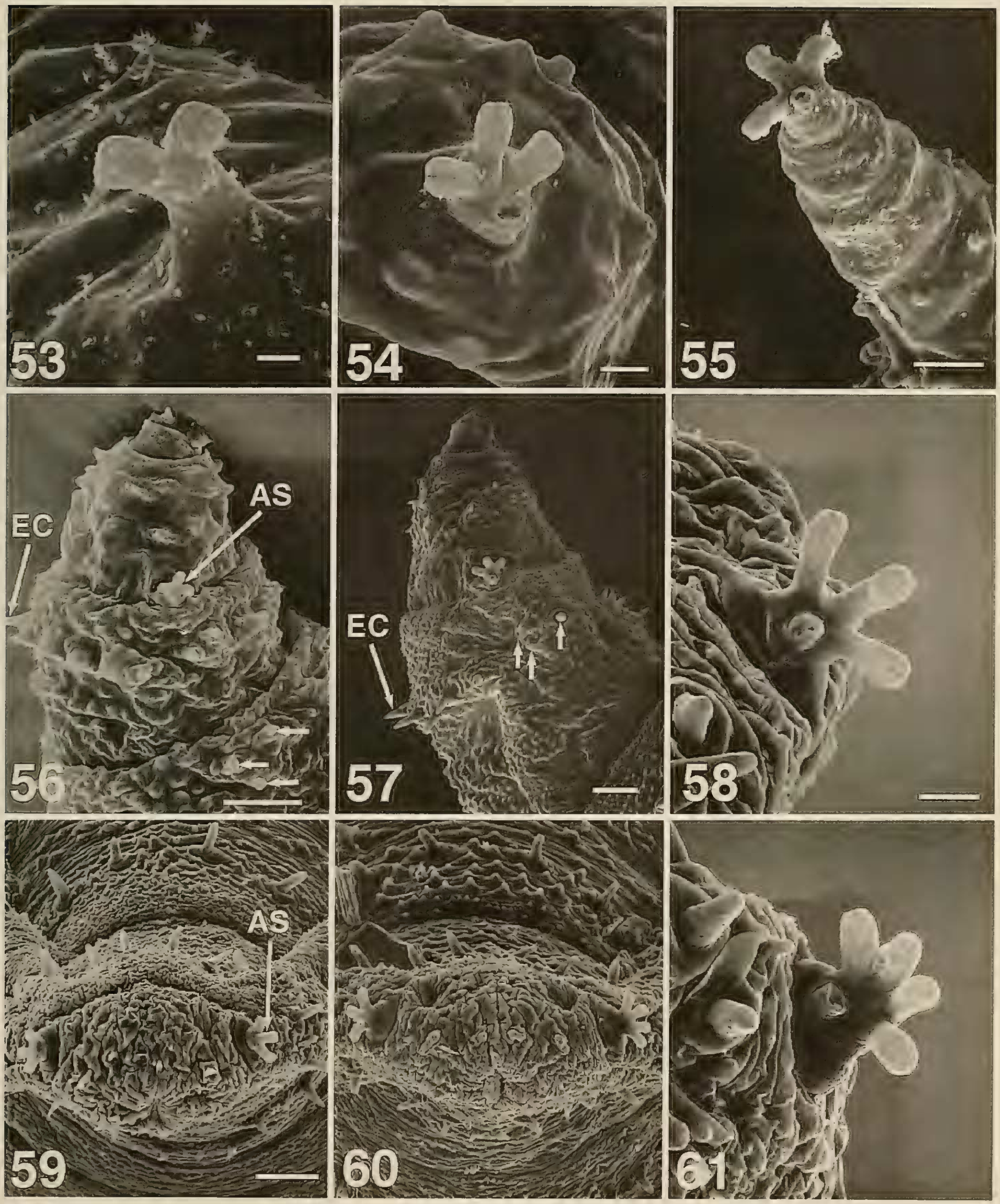
Segment VIII, laterally with 3 enlarged, stubby chaetoids present in triangular arrangement.

Discussion

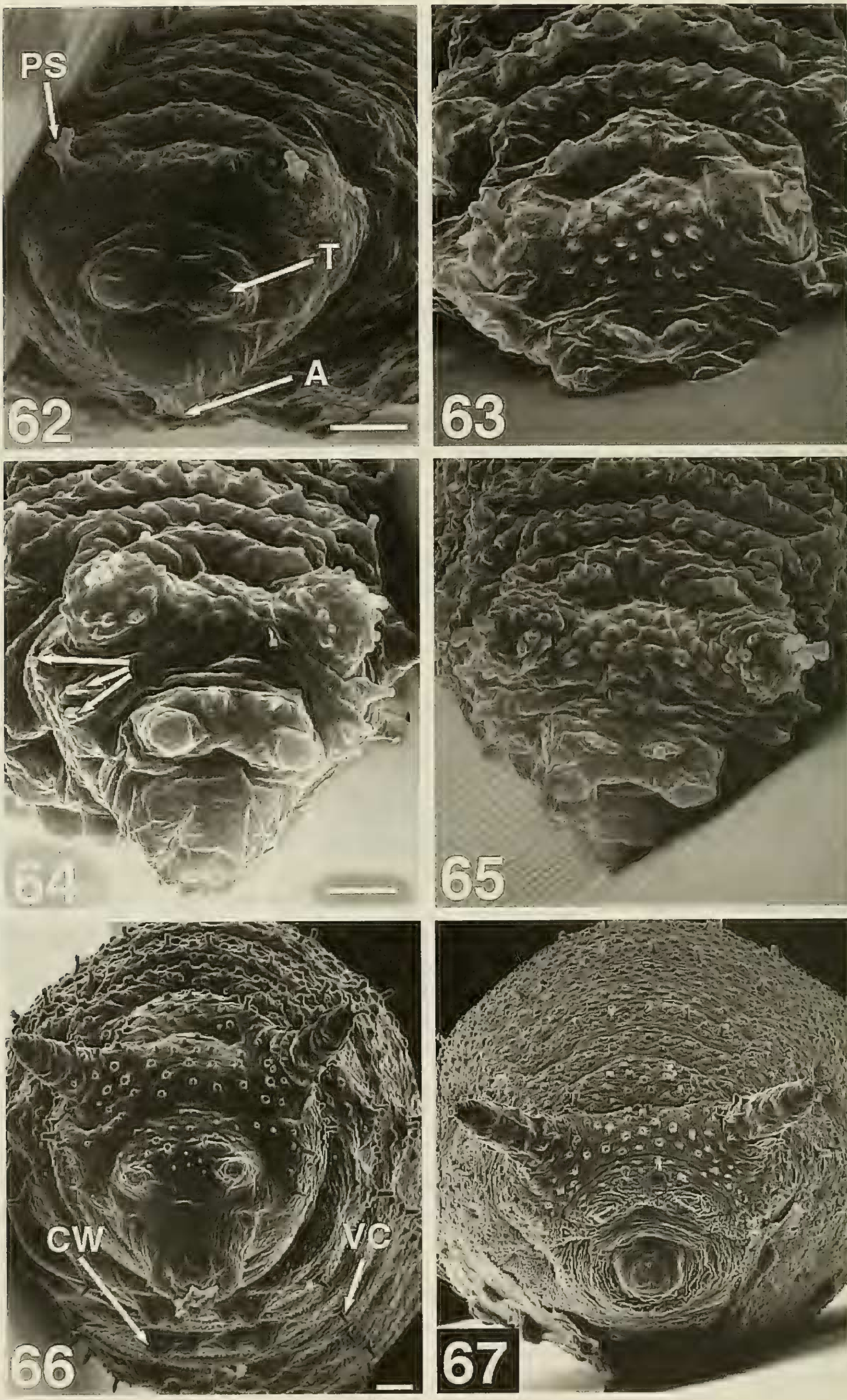
In most cases, differences between the populations were not profound, but at least subtle differences were discovered in all stages and instars. Character differences in the egg stage involve chorionic reticulation patterns and the anastamosing of longitudinal ridges. Those of the larval and puparial stages involved surface sculpturing, and the nature and definition of chaetoids.

The egg of *Leucopis gaimarii* 'Central Ferry' is most distinctly different from that of the other two populations in the chorionic latticework, where the pore density is highest and the average pore diameter is smallest. Eggs of both *L. ninae* and *L. gaimarii* 'Anatone' have similar chorionic pore densities; however, in *L. ninae,* the ratio of pore diameter to inter-pore distance is typically less than 1:1, and all pores appear smoothed and rounded. In *L. gaimarii* 'Anatone', the ratio of pore diameter to inter-pore distance is greater than 1:1, and all pores usually display an angular appearance. Eggs of *L. gaimarii* 'Central Ferry' are also unique in that the dorsal longitudinal ridges are closely parallel and unbranched within the transverse dorsomedian area. In the other two, ridges appear subparallel, with at least occasional anastamosing within the dorsomedian area.

Differences among first larval instars of the three species are associated largely with the nature and pattern of small chaetoids on the dorsal aspect of the anterior and posterior pseudosegments of segments 2–VII. In both populations of *L. gaimarii,* the chaetoids are contiguous and arranged in a braided pattern, while those of *L. ninae* are



Figs. 53–61. Spiracles. 53, *Leucopis gaimarii* 'Anatone,' first instar, posterior spiracular process (scale bar = 0.005 mm). 54, *L. ninae,* second instar, posterior spiracular process (scale bar = 0.01 mm). 55, *L. ninae,* third instar, posterior spiracular process (scale bar = 0.05 mm). 56, *L. gaimarii* 'Central Ferry,' second instar, segments 1–3, lateral (scale bar = 0.05 mm). 57, *L. ninae,* third instar, segments 1–2, lateral (scale bar = 0.05 mm). 58, *L gaimarii* 'Anatone,' puparium, anterior spiracular process (scale bar = 0.02 mm). 59, *L. ninae,* puparium, frontal (scale bar = 0.05 mm). 60, *L. gaimarii* 'Central Ferry,' puparium, frontal. 61, *L. gaimarii,* 'Central Ferry,' anterior spiracular process. Abbreviations: AS = anterior spiracular process; EC = elongated chaetoid; unlabelled arrows = triangular arrangement of enlarged chaetoids.



Figs. 62–67. Segment VIII, posterior. 62, *Leucopis ninae,* first instar (scale bar = 0.05 mm). 63, *L. gaimarii* 'Central Ferry,' first instar. 64, *L. ninae,* second instar (scale bar = 0.05 mm). 65, *L. gaimarii* 'Central Ferry,' second instar. 66, *L. ninae,* third instar (scale bar = 0.1 mm). 67, *L. ninae,* puparium. Abbreviations: A = anus; CW = creeping welt; PS = posterior spiracle; T = tubercle; VC = ventrolateral chaetoid; unlabelled arrows = triangular arrangement of enlarged chaetoids.

separated. In addition, the chaetoid density is higher in *L. gaimarii* 'Central Ferry' than in *L. gaimarii* 'Anatone'. The chaetoid density of *L. ninae* is intermediate to those for the two populations of *L. gaimarii.*

The second instar of *L. ninae* is very distinctive. Elongated, spinule-like chaetoids are present in the transverse row of the middle pseudosegments and on the lateral swellings of this species. Both populations of *L. gaimarii* have enlarged, stubby chaetoids in the transverse row and on the swellings. These chaetoids are more well-defined in the 'Central Ferry' population than in the 'Anatone' population. Also, in *L. ninae,* the chaetoids on the anterior and posterior pseudosegments are poorly-defined and separated. By comparison, these chaetoids are contiguous in both populations of *L. gaimarii,* but are poorly-defined only in the 'Anatone' population. The lateral swelling of *L. gaimarii* 'Central Ferry' is also distinctive from that present in the other two, with a dense covering of small, well-defined chaetoids. The other two populations appear quite similar to one another in this character, with only sparse, small, poorly-defined chaetoids. In addition, for *L. ninae,* the small chaetoids of the posterior pseudosegment of segment VIII are distinctive. The chaetoids are poorly-defined, separated, and sparse ($\approx$14) between the posterior spiracular processes. Both populations of *L. gaimarii* have more than 20 well-defined, contiguous or crowded chaetoids between the spiracles.

The most distinctive differences among larvae were found in the third instar. In only *L. ninae* is the transverse row of enlarged chaetoids still clearly visible. As in the second instar, these chaetoids are elongated, spinule-like, and distinctly larger than the other chaetoids present. In both *L. gaimarii* populations, the dorsal chaetoids of all three pseudosegments are stubby and subequal in size. Also, in *L. ninae,* the small chaetoids on the dorsum of the anterior and posterior pseudosegments are well-defined, separated, and dense, numbering over twice that in either *L. gaimarii* population. The chaetoids of *L. gaimarii* are poorly-defined, with those of the 'Anatone' population appearing contiguous in a braided pattern. In *L. ninae* the lateral swellings have 3 elongated, spinule-like chaetoids in a triangular arrangement. By comparison, the chaetoids are short and stubby in both *L. gaimarii* populations. In lateral view, part of the ventral surface is visible. This surface of *L. ninae* is densely covered with tiny, well-defined chaetoids, while that of either population of *L. gaimarii* is sparsely studded with tiny, poorly-defined chaetoids. In addition, the ventrolateral chaetoid is elongated and spinule-like only in *L. ninae.*

The characters of the puparial stage are essentially the same as for the third larval instar, with only minor differences. For example, the small, separated chaetoids of the third larval instar of *L. gaimarii* 'Central Ferry' appear both contiguous and braided in the puparium. Additionally, the small chaetoids of both populations of *L. gaimarii* appear more flattened or decumbent.

This study serves to illustrate the inter- and possibly intra-specific variability of *Leucopis* (*s. str.*) in the immature stages. Although the adults of the two populations of *L. gaimarii* could not be differentiated (Tanasijtshuk 1996b), the immatures, which were reared simultaneously under identical conditions, were distinguishable. Likewise, biological differences were apparent (Gaimari and Turner 1996). These consistent differences in immatures suggest that there is likely some real difference between the populations. Because *Diuraphis noxia* is a recently introduced cereal aphid in the Pacific Northwest, we can assume that it is not a native host for either population of *L. gaimarii.* In fact, specimens now identifiable as *L. gaimarii* had been collected in the region as early as 1912, with some from aphids on *Elymus* (Poaceae) (Tanasijtshuk 1996b), well before the introduction of the *D. noxia.* A possible explanation for the differences in the immature stages is that the two populations were recently separated, perhaps by host or elevational preferences, and had begun to diverge when *D. noxia* entered the region and provided a suitable, unexploited resource for both of them. The characters of the immature stages could have diverged before those of the adults due to the different evolutionary pressures on functional morphology applied while feeding in different host homopteran colonies. Alternatively, *L. gaimarii* may have some degree of populational plasticity in the immature stages, due to any number of possible factors, including those mentioned above. According to Tanasijtshuk (1996b), the adults were also quite variable in certain characteristics, but not as divided into distinct populations. Nevertheless, the possibility that the populations are somehow distinct warrants further exploration, perhaps using allozyme comparisons to look for fixed gene loci, or simple cross-breeding experiments.

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